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Dieback intensity but not functional and taxonomic diversity indices predict forest productivity in different management conditions: Evidence from a semi-arid oak forest ecosystem

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Abstract: The relationships between different aspects of diversity (taxonomic, structural and functional) and the aboveground biomass (AGB) as a major component of global carbon balance have been studied extensively but rarely under the simultaneous influence of forest dieback and management. In this study, we investigate the relationships between taxonomic, functional and structural diversity of woody species (trees and shrubs) and AGB along a gradient of dieback intensity (low, moderate, high and no dieback as control) under two contrasted management conditions (protection by central government vs. traditional management by natives) in a semi-arid oak (*Quercus brantii* Lindl.) forest ecosystem. AGB was estimated and taxonomic diversity, community weighted average (CWM) and functional divergence indices were produced. We found that the aerial biomass was significantly higher in the intensively used area (14.57 (±1.60) t/hm²) than in the protected area (8.70 (±1.05) t/hm²) due to persistence of some large trees but with decreasing values along the dieback intensity gradient in both areas. CWM of height (H), leaf nitrogen content (LNC) and leaf dry matter content (LDMC) were also higher in the traditional managed area than in the protected area. In contrast, in the protected area, the woody species diversity was higher and the inter-specific competition was more intense, explaining a reduced H, biomass and LDMC. Contrary to the results of CWM, none of the functional diversity traits (FDvar) was affected by dieback intensity and only FDvar values of LNC, leaf phosphorus content (LPC) and LDMC were influenced by management. We also found significantly positive linear relationships of AGB with CWM and FDvar indices in the protected area, and with taxonomic and structural diversity indices in the traditional managed area. These results emphasize that along a dieback intensity gradient, the leaf functional traits are efficient predictors in estimating the AGB in protected forests, while taxonomic and structural indices provide better results in forests under a high human pressure. Finally, species identity of the dominant species (i.e., Brant's oak) proves to be the main driver of AGB, supporting the selection effect hypothesis.

Keywords: environmental stress; sudden oak dieback; degradation; conservation; selection effect hypothesis

1 Introduction

Forests in many regions over the world are exposed to numerous destructive factors of anthropic origin (Heydari et al., 2012; Chaturvedi et al., 2017a; Menezes et al., 2021), putting at risk their biomass production (Chaturvedi et al., 2012; Milkias and Toru, 2018) and their main ecosystem functions (Zhang et al., 2017; Bochet et al., 2021; Chaturvedi et al., 2021). Since 2000, a dangerous phenomenon, called oak (*Q. brantii*) decline (Kamata et al., 2002; Lloret et al., 2004; Morillas et al., 2012; Attarod et al., 2017; S ánchez-Salguero et al., 2020) has occurred in many oak forests around the world (Mc Dowell et al., 2008), and especially in the Mediterranean region. In that respect, a gradual dieback of semi-arid oak formations was observed in the Zagros forests of western Iran, which are among the oldest oak forest reserves in the world with a remarkable ecological value (Shiranvand and Hosseini, 2020).

Although the exact cause of this forest dieback has not been determined, most studies have emphasized the role played by climate change (in particular prolonged drought periods), habitat degradation (including depletion of soil nutrients and moisture), non-adaptive management, and pest and disease outbreaks (Brasier and Scott, 1994; Kamata et al., 2002; Choi, 2011; Touhami et al., 2019). The impact of forest dieback on growth and biomass accumulation is influenced by a wide set of factors, and among them, species diversity can play a significant role (Keesing et al., 2006; Mitchell et al., 2014). For instance, severe droughts can significantly reduce tree growth and biomass accumulation, however, this effect varies according to tree diversity in different biomes (Hogg et al., 2008; Grossiord et al., 2014a, b; Ogaya et al., 2015). In general, a positive relationship between forest biomass production and tree species diversity is agreed upon by most researchers (e.g., Hulvey et al., 2013; Chaturvedi and Raghubanshi, 2015; Ali et al., 2019a), although changes in direction or absence of a relationship can also occur (Zhang et al., 2017; Wekesa et al., 2019). This process can be explained by complementarity in ecological traits among species (Zhang et al., 2012; Jactel et al., 2017) and underlines the concept of the functional diversity (FD) that refers to the amount, range, distribution and relative frequency of functional characteristics of the species in the ecosystem (D áz et al., 2007). For instance, in a forest system, functional traits and structural characteristics of forest stands (such asdiameter and height differentiation of trees) could influence the ecosystem functions (e.g., AGB) along with abiotic factors, human (Chaturvedi et al., 2017b; Ma et al., 2019) and natural disturbances (Barlow et al., 2003).

However, it is noteworthy that numerous studies have recorded a variation of the diversity-ecosystem function relationships based on the type of forest ecosystems, which can be negative (Ruiz-Jaen and Potvin, 2011; Lasky et al., 2014; Azad et al., 2020) or positive (Zhang et al., 2017; Li et al., 2018). This apparent lack of consistency indicates that various factors, such as heterogeneity of habitat environmental conditions, type and structure of vegetation, geographical scale (Isbell et al., 2018), management measures, land use change and interactions with climate (Peters et al., 2019) can affect the relevant mechanisms influencing the diversity-ecosystem function relationships (Zhang et al., 2016; Brancalion et al., 2019; Wekesa et al., 2019).

In general, the relationships of species diversity and traits with different ecosystem functions can be expressed using two main hypotheses: the niche complementarity and the selection effect hypotheses (Grime, 1998). The niche complementarity hypothesis is based on the assumption that communities with functionally diverse species are better able to use limited environmental resources (Diaz et al., 2007). The differences in the functional characteristics of plants (functional diversity) reduce the species niches overlap (lower competition) in capturing available resources, leading to the maximization of the processes of matter transformation and energy flux (Zhang et al., 2012). On the other hand, in the selection effect hypothesis, the effects of a species being

proportional to its relative abundance in the community and ecosystem function are predominantly influenced by the dominant species that present more efficient functional traits compared with other plants (Grime, 1998). It implies that ecosystem functions are controlled by the presence or absence of the dominant species, whereas the addition or elimination of other plants does not have a great influence on ecosystem function. Studies supporting these hypotheses have used indices based on the frequency and value of functional traits such as the functional divergence (FDvar) and community weighted mean (CWM) of a trait value (Bíáet al., 2014; Ali et al., 2017; Rawat et al., 2019). For example, the carbon and AGB storage are positively correlated to the CWM of trees with a high potential maximum diameter (Fichtner et al., 2015; Chiang et al., 2016), because these trees are able to use more environmental resources, such as light and moisture, and to be more efficient competitors than their neighbors (Kraft et al., 2008; Chiang et al., 2016).

Both functional and taxonomic diversity, by reflecting stand structure can be efficient indicators of AGB (Dănescu at al., 2016; Cheng and Liu, 2017). In addition, the forest structure plays a major role in determining ecosystem function, so any factor that changes this structure (including forest dieback) can change the diversity-biomass relationship (Bohn and Huth, 2017; O'Connor et al., 2017), although this point requests further investigations in disturbed forest systems. More research on diversity-ecosystem function relationships in different ecosystems is also needed, in particular to understand how these relationships are affected by changing natural forest structure, management practices and natural and anthropogenic disturbances. In this study, we investigate the relationships between functional, taxonomic and structural diversity of woody species and AGB in a semi-arid oak forest of western Iran. We hypothesize that these relationships can be influenced by dieback intensity and management conditions. More specifically, our questions are the following: (1) Is the effect of dieback intensity on AGB and biotic indices (taxonomic, functional and structural diversity) affected by management conditions? Two contrasted management conditions were tested: protection vs. traditional management. (2) How much variation in the ecosystem production can be explained by taxonomic, functional and structural diversity characteristics along a gradient of dieback intensity under different management conditions? (3) Which is the best combination of multiple metric of taxonomic, functional and structural diversity regarding dieback intensity under different management conditions? And (4) can the relationships between taxonomic, functional and structural diversity and AGB be expressed by the niche complementarity and selection effect hypotheses?

2　Material and methods

2.1　Study area

This study was conducted in oak forests of Ilam City in western Iran known as Zagros forests, which are one of the oldest continuous oak forests in the world. For this purpose, two adjacent forest areas with the same flat physiographic conditions (with an altitude range from1279 to 1450 m a.s.l. and generally flattopography; average slope<20%) were selected (Fig. 1), and named by their level of disturbance and management conditions (traditional management by natives) and protected area (protection by government). Both areas were initially composed of a dense forest cover based on documents of the Natural Resources Office and interviews with natives (Heydari et al., 2013).

The selected forest areas were exposed to human disturbances (e.g., firewood exploitation, grazing and land-use change) (Heydari et al., 2014), but with some differences between the two areas. Before enforcing protection in the area named protected area, a significant number of big trees were cut down for extracting a large quantity of wood biomass to meet various needs of the population (in particular exploited by a migrant population, charcoal smugglers and temporary ranchers). In contrast, the traditional managed area has been used by nomads and neighboring rural areas for agriculture and animal husbandry. The management of this forest area followed

traditional practices: big trees were preserved mostly because they provided shade for temporary structures (huts and tents), and their high acorn production was used for livestock feeding. In contrast, coppice oak and the remaining small woody species like *Crataegus pontica* K. Koch., *Cerasus microcarpa* (C. A. Mey.) Boiss. and *Daphne mucronata* Royle were regularly cut down (mostly for firewood and for making hedges for livestock).
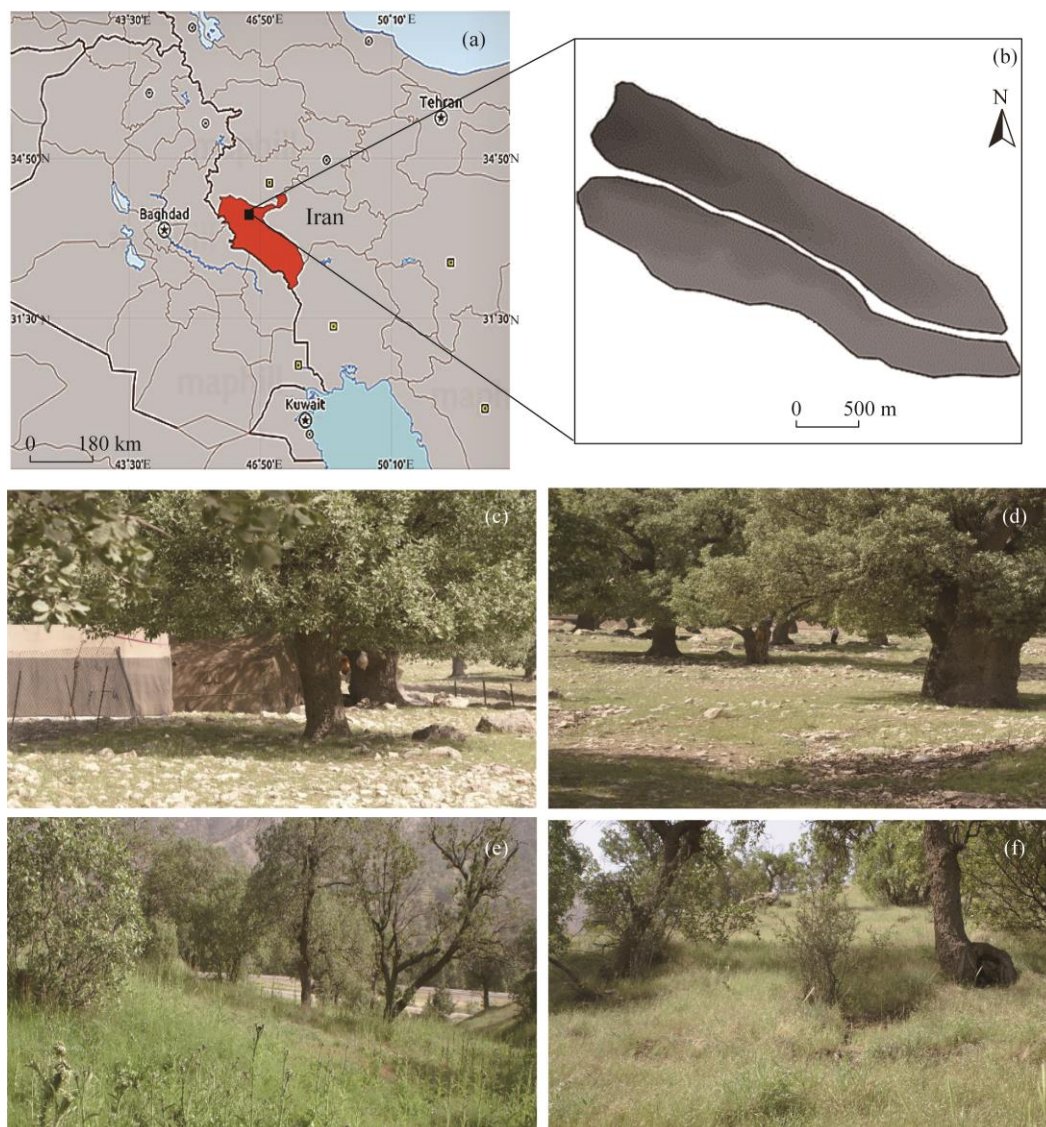
Fig. 1 (a), location of the study area in the Ilam Province, Iran; (b), map of the two studied areas; views of the traditional managed area (c, d) and protected area (e, f).

In the so-called protected area today, the degradation was mostly related to war refugees, non-foresters, and wood and coal smugglers. These people did not understand the need to preserve dominant, ancient and large trees, such as seed-origin oak and pistachio trees. Therefore, many large trees were cut down by them that gradually developed the oak coppice form. After a period of intense exploitation, the conditions of ownership changed in the protected area: lands were taken back from private ownership by the Natural Resources Office after implementation of national policies in 1963. After this step, the protection measures were applied (Valipour et al., 2014). The area was fenced and supervised by forest guards to prevent any disturbing factors (e.g.,

fire, grazing and logging). In contrast, the other part (i.e., traditional managed area) continued to be traditionally exploited by the local people and nomads. The dominant species of these forests is the Brant's oak (*Quercus brantii*) that associated with different woody species, such as *Pistacia atlantica* Desf., *Acer monspessulanum* subsp. Cinerascens (Boiss.) Yalt., *Crataegus pontica* K. Koch, *Cerasus microcarpa* Andrz. ex DC and *Daphne mucronata* Royle. In the traditional managed area, often large old oak and pistachio trees were present, while other woody species were very rare. Since 2001, a phenomenon called oak dieback occurred in the Zagros forests, including the forests of the study area, which led to the drying up of trees especially oaks with different intensities. Factors causing this forest decline are not exactly known, but are supposed to be linked to climate change, in particular, recurrent and prolonged drought periods (Goodarzi et al., 2019; Shiravand and Hosseini, 2020). Trees with symptoms of decline of different intensities are scattered in the study area and oak is the main species affected.

The most abundant soil types based on FAO classification are Lithosols, i.e., shallow soils with low fertility and low water holding capacity. According to the climatic data (1999–2015) of the nearest meteorological station (Eyvan station, 33°45′N and 46°21′E; 1320 m a.s.l), the mean annual precipitation and annual mean temperature are 653 mm and 17°C, respectively. This region is described as sub-Mediterranean with a high seasonality of monthly precipitation distribution. More than 50% of precipitation occurs in winter, 32% in autumn and 14% in spring, whereas the summer period is particularly dry (May–October).

2.2 Experimental design

The two forest areas (traditional managed (degradation) and protected) were sampled using 80 plots with an area of 1000 m^2 (40 plots in each area, distance between plots varies from 500 to 1000 m) distributed in four forest dieback classes (i.e., 10 plots per class in each area) that were defined as follows. First, in each plot, the ratio of the dried canopy part to the total crown of each tree was determined visually as a measure of dieback intensity (*I*) and then weighed by the frequency (*F*) of the tree species (percentage of the crown cover). Finally, the dieback intensity of each plot was determined from the total weighted dieback of all the individuals of the plot (Eq. 1) and categorized into four classes of dieback intensity: no, low, moderate and high dieback (Table 1; Fig. 2).

$$\mathrm{DI} = \sum_{i=1}^{n} I_i \times F_i, \tag{1}$$

where, DI is the total dieback intensity in each plot; I_i and F_i are the dieback intensity and the frequency of species *i*, respectively. The resulting values of DI were used to establish four classes: 0%≤DI<10%, no dieback; 10%≤DI≤35%, low intensity dieback; 36%≤DI<65%, moderate intensity dieback; and 65%≤D≤100%, high intensity dieback (Table 1).

2.3 Estimation of AGB

We measured the diameter at breast height (DBH) and height (H) of all woody species in each plot. In the absence of any models to estimate AGB for our species and conditions, AGB of each

Table 1 Dieback intensity classes

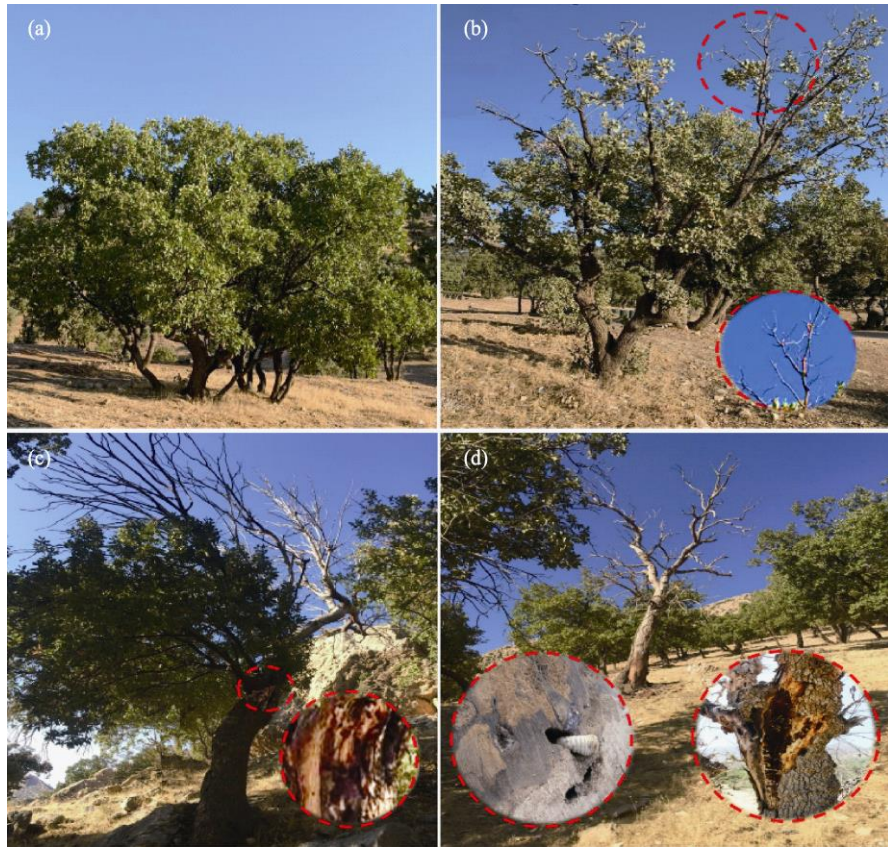| Dieback intensity class			
≥65%	36%–65%	10%–35%	≤10%
High intensity dieback	Moderate intensity dieback	Low intensity dieback	No dieback or control
Signs of canopy dryness can be seen all over the tree canopy and in total about 3/4 of the tree canopy has dried; symptoms such as deep cracks, numerous holes, decay and disease can be seen all over the trunk, and sometimes half of the trunk is gone.	Signs of canopy dryness can be seen in the tree canopy and in total about 1:2 of the tree canopy has dried; symptoms such as cracks, decay and disease can be seen in parts of the trunk.	Signs of canopy dryness can be seen in the tree canopy and in total about 1:4 of the tree canopy has dried; there are no other symptoms such as cracks, decay and disease in the trunk.	In late spring, there are no signs of canopy dryness in the tree and the crown and only few dry branches are seen.

Fig. 2 Trees in the four classes of dieback intensity. (a) no dieback; (b) low dieback; (c) moderate dieback; (d) high dieback.

woody species with a DBH≥5 cm was estimated using an allometric relationship (Eq. 2) by Chave et al. (2014). This model covers a wide range of climatic conditions and vegetation types across the world. Because of its high genericity, the model was also used for drier forest systems (Ayma-Romay and Bown, 2019; Tetemke et al., 2019). In fact, the model includes three general variables that are easy to establish: a measure of tree size (DBH), a site-specific environment stress factor (EF) and wood density (WD, g/cm^3). Finally, the amount of AGB (t/hm^2) for the plot was obtained from the sum of all individuals.

$$AGB=\exp\{-1.803-0.976(EF)+0.976\times\ln(\rho)+2.673\times\ln(DBH)-0.0299\times(\ln(DBH))^2. \quad (2)$$

The EF and climatic water deficit (CWD) were computed using Equations 3 and 4 (Chave et al., 2014).

$$EF=(0.178\times TS-0.938\times CWD-6.61\times PS)\times10^{-3}, \quad (3)$$

$$CWD=\sum_{i=1}^{n}\min(0, P_i-ET_i), \quad (4)$$

where TS is the temperature seasonality: the standard deviation (SD) of the monthly mean temperature over a year, expressed in degrees Celsius multiplied by 100; PS is the precipitation seasonality: the standard deviation (SD) of the monthly mean precipitation over a year, expressed in millimeters multiplied by 100; CWD is the climatic water deficit computed by the summing the difference between monthly precipitation (P_i) and monthly evapotranspiration (ET_i), only when this difference is negative. In our conditions, EF was equal to 2.086.

2.4 Measurement of functional traits

To measure functional diversity at plot level, we selected and measured traits that were directly related to AGB according to previous studies (Inagaki and Tange, 2014; Finegan et al., 2015; Ali

and Yan, 2017). For each woody species, two branches of different crown height classes (bottom, middle and top) were selected in the south-facing part of the crown, and a total of twenty well grown and without damage leaves were sampled (Cornelissen et al., 2003; Perez-Harguindeguy et al., 2013; Ali et al., 2019b). The leaves were immediately stored in an ice box after labeling for measurements in the laboratory. In the laboratory, the fresh weight and the dry weight (48 h at 70 °C) were measured (±0.01g). The areas of the fresh collected leaves (mm^2) were also measured using a leaf area meter (Model CI-203, CID Bio-Science Inc., Camas, WA). LDMC (mg/g) was computed as the oven dry mass of a leaf, divided by its fresh mass. Specific leaf area (SLA) was obtained from the ratio of leaf area to leaf dry weight (Cornelissen et al., 2003; Perez-Harguindeguy et al., 2013). For each woody species, we collected one wood sample on ten individuals at 1-m height using a tree corer. All woody samples were dried in an oven at 105 °C for 24 h (Henry et al., 2010). WD (g/cm^3) of each sample was determined as the ratio of dry weight divided by the volume that was measured using the change in volume after immersion in distilled water in a beaker. LPC and LNC (mg/g) were determined using the phosphomolybdic blue colorimetric technique (Anderson and Ingram, 1993) and the Kjeldahl method (Bradstreet, 1965), respectively.

2.5　Measurements of taxonomic, structural and functional diversity indices

To quantify the woody species (trees and shrubs) diversity at plot level, we used three indices including species richness (number of woody species per sample or S), Shannon-Wiener diversity index (H'; Eq. 5) and evenness (E; Eq. 6).

$$H' = -\sum_{i=1}^{s} p_i \ln p_i, \tag{5}$$

$$E = H' / \ln(S), \tag{6}$$

Where p_i is the proportion of species i and S is the total number of woody species. In this study, to distinguish the effects of dominant species (selection effect) and diversity (niche complementary), we used two indices: CWM and FDvar (Tahmasebi et al., 2017; Rawat et al., 2019). CWM was calculated as the mean trait value in the community, weighted by the abundance of the species (Garnier et al., 2004). FDvar was computed using the variance among the traits values of the plant species recorded on a plot and weighted by the abundance of each species in the community (Mason et al., 2005). Two different types of structural indices of woody species were produced at plot level. The species mingling index was calculated using Equation 7 (Pommerening, 2002):

$$M_j = \frac{1}{n} \sum_{i=1}^{n} V_{ij} M_j \in [0,1], \tag{7}$$

where M_j is the species mingling index; n is the number of the nearest neighbors (n=3); V_{ij}=1, if the reference tree j and neighbor tree i are different tree species, otherwise, V_{ij} = 0. Lower values of this index reflected purity or very low presence of other woody species.

　H and diameter differentiation index (T_{ij}) were calculated following Equation 8. In each plot, a woody species was randomly selected as the reference tree (i) and the three nearest neighbor woody species (j) were determined.

$$T_i = \frac{1}{n} \sum_{i=1}^{n} T_{ij},$$

$$T_{ij} = 1 - \frac{\min(\mathrm{DBH}_i \times \mathrm{DBH}_j)}{\max(\mathrm{DBH}_i \times \mathrm{DBH}_j)} \text{ or } T_{ij} = 1 - \frac{\min(\mathrm{Height}_i \times \mathrm{Height}_j)}{\max(\mathrm{Height}_i \times \mathrm{Height}_j)}, T_i \in [0,1] \cdot \tag{8}$$

　These equations were used for the three pairs of reference woody-neighbor woody species and the T_{ij} indices were obtained as the mean of the three individual calculations. The higher value of the index (close to 1), the higher diversity in terms of tree size.

2.6　Statistical analysis

After examining the preconditions of normality (Shapiro-Walk test) and homogeneity of variance

(Levene test), the effects of management (protection vs. traditional management), dieback intensity and their interactions on CWM and FDvar and on structural and diversity indices were tested using two-way analysis of variance (ANOVA). Post-hoc tests were then applied using t-student and Duncan tests. Linear regression was used to predict the AGB as function of structural diversity, taxonomic and functional diversity indices. All variables were standardized (min=0 and SD=1) to improve interpretability of regression coefficient (Schielzeth, 2010). To detect the best combination of AGB predictors including taxonomic (richness, Shannon-Wiener diversity and evenness), we produced functional composition and structural diversity (height, diameter differentiation and mingling) indices and dieback intensity, multiple linear mixed models using nlmeR package (Pinheiro et al., 2017). Then, to select the best indices in AGB predictors, the relative importance was calculated using MuMIn R package (Barton, 2016) and introduced to structural equation modeling (SEM) using lavaan R package (Rosseel, 2012). As there was only one woody species in many of sampling plots in the traditional managed area, the FDvar of different traits could not be calculated, so this index was removed from the final SEM in both areas. In addition, dieback intensity was introduced in the model as a fix factor using four ordinal categories including control (no dieback), low, moderate and high dieback coded by 1–4, respectively. The best-fit SEMs were assessed using chi-square (χ^2) test (i.e., $P>0.05$), Bentler's comparative fit index and goodness of fit index (i.e., CFI and GFI), coefficient of determination (R^2), and root mean square error of approximation (RMSEA). To obtain the best fit SEMs, we selected the two variables with the highest relative importance in each category and the best combination of variables using a try and error approach. All statistical analyses were performed using R v3.6.3 software.

3 Results

3.1 Effects of management and dieback intensity on AGB and diversity indices

AGB was affected by management (F=14.20; $P<0.001$), and it was higher in the traditional managed (14.57 ($\pm$1.60) t/hm^2) than in the protected area (8.70 ($\pm$1.05) t/hm^2). It was also significantly influenced by dieback intensity (F=12.89; $P<0.001$) with decreasing values along the dieback intensity gradient in both areas (Fig. 3). However, we found no significant interaction between management and dieback intensity (F=2.09; P=0.109).
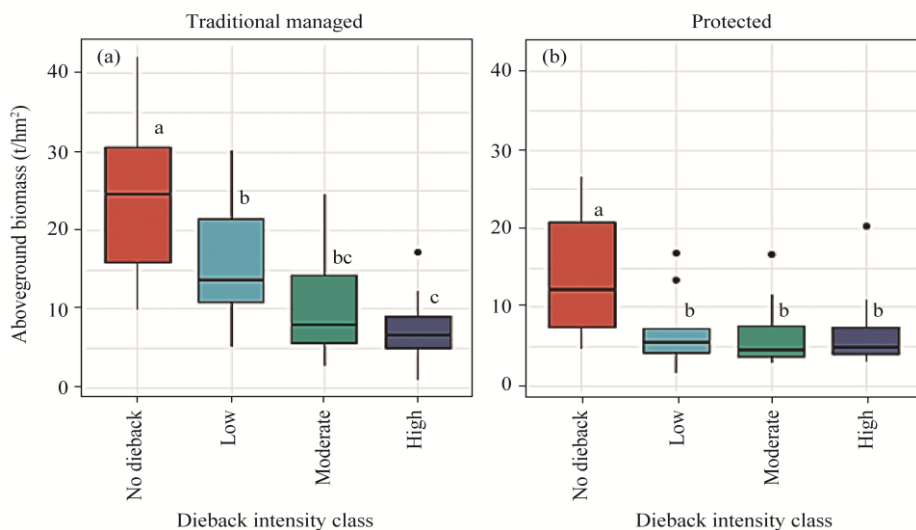

Fig. 3 Mean aboveground biomass values under different dieback intensity classes (control, low, moderate and high dieback) in the traditional managed (a) and protected (b) areas. Different lowercase letters indicate significant differences among different dieback intensity classes within the same area at $P<0.05$ level.

CWM of all functional traits (LPC, LNC, H, LDMC, SLA and WD) were significantly affected by the type of management, dieback intensity and their interaction (Table 2). In contrast, FDvar of some leaf characteristics, such as LNC, LPC and LDMC were only affected by the type of management, while dieback intensity had no significant effect, whatever be the traits.

Table 2 Results of the generalized linear model with protection, dieback intensity and their interaction on CWM and FDvar functional traits

	df	CWM of LPC		CWM of LNC		CWM of H	
		F	P	F	P	F	P
Management (A)	1	117.60	<0.001	148,042	<0.001	10,098	<0.001
Dieback intensity (B)	3	3.55	0.019	6.79	<0.001	6.89	<0.001
A×B	3	3.55	0.019	7.31	<0.001	7.27	<0.001

	df	CWM of LDMC		CWM of SLA		CWM of WD	
		F	P	F	P	F	P
Management (A)	1	167,215	<0.001	446,409	0.001	4.02	0.049
Dieback intensity (B)	3	7.01	<0.001	3.72	0.015	4.77	0.004
A×B	3	7.22	<0.001	3.89	0.012	6.55	0.001

	df	FDvar of LPC		FDvar of LNC		FDvar of H	
		F	P	F	P	F	P
Protection (A)	1	17.170	<0.001	7.370	0.009	5.930	0.190
Dieback intensity (B)	3	0.152	0.928	1.120	0.351	1.130	0.348
A×B	3	0.216	0.806	0.137	0.872	0.002	0.998

	df	FDvar of LDMC		FDvar of SLA		FDvar of WD	
		F	F	P		F	P
Protection (A)	1	8.32	0.238	0.628		1.170	0.282
Dieback intensity (B)	3	0.56	0.728	0.540		2.780	0.052
A×B	3	0.51	0.088	0.916		0.278	0.758

Note: CWM, community weighted average; FDvar, functional divergence; LPC, leaf phosphorus content; LNC, leaf nitrogen content; H, height; LDMC, leaf dry matter content; SLA, specific leaf area; WD, wood density.

CWM of LDMC, LNC and H were higher in the traditional managed area, while CWM values of SLA and LPC were higher in the protected area. CWM of LPC value was the highest in the low and moderate dieback intensities in the protected area, while there was no significant difference between the different dieback intensities in the traditional managed area (Table 3).

There was no significant difference among the different dieback intensity classes in the protected area for CWM of LNC, LDMC and H. In contrast, the highest values of CWM of LNC and LDMC occurred in the low dieback intensity class and in the high dieback intensity of the traditional managed area for CWM of H (Table 3). FDvar of LNC and LDMC and FDvar of LPC were higher in the protected and traditional managed area, respectively, while there was no significant difference among the different dieback intensities for these attributes (Table 3).

All taxonomic diversity indices were affected by management, dieback intensity and their interaction ($P<0.001$). Structural diversity indices were similarly affected by management and dieback intensity, while the interaction was only significant on diameter ($F=7.32$; $P<0.001$) and height ($F=13.65$; $P<0.001$) differentiation indices (Table 4).

The woody species richness varied from 1 to 2 (*Q. brantii* or *Q. brantii*or and *P. atlantica*) in the traditional managed area, whereas it varied from 2 to 6 in the protected area (*Q. brantii*, *P. atlantica*, *A. monspessulanum* subsp. *cinerascens*, *C. pontica*, *C. microcarpa* and *D. mucronata*).

Table 3 Comparison of mean of CWM and FDvar of functional traits under different dieback intensities in the traditional managed and protected areas

Functional diversity index	Traditional managed				Protected			
	No dieback or control	Low intensity dieback	Moderate intensity dieback	High intensity dieback	No dieback or control	Low intensity dieback	Moderate intensity dieback	High intensity dieback
CWM of LPC	0.238±0.00[c]	0.24±0.00[c]	0.239±0.00[c]	0.240±0.00[c]	1.114±0.13[b]	1.985±0.27[a]	1.834±0.28[a]	1.174±0.23[b]
CWM of LNC	2.72±0.014[b]	2.85±0.000[a]	2.76±0.020[b]	2.49±0.008[c]	0.24±0.001[d]	0.24±0.001[d]	0.24±0.001[d]	0.24±0.001[d]
CWM of H	9.02±0.150[c]	9.29±0.000[b]	9.36±0.210[b]	9.72±0.080[a]	2.77±0.006[d]	2.74±0.006[d]	2.74±0.012[d]	2.77±0.007[d]
CWM of LDMC	570.44±3.11[d]	586.66±0.00[a]	577.53±4.29[c]	580.93±1.72[b]	9.27±0.06[e]	8.96±0.13[e]	9.05±0.14[e]	9.35±0.08[e]
CWM of SLA	7.52±0.04[c]	7.74±0.00[c]	7.62±0.05[c]	7.72±0.02[c]	581.11±0.80[a]	574.93±1.90[b]	575.98±2.40[b]	581.25±1.20[a]
CWM of WD	0.81±0.012[e]	0.87±0.000[a]	0.83±0.016[cde]	0.86±0.006[ab]	0.84±0.004[bcd]	0.82±0.009[de]	0.82±0.01[de]	0.85±0.006[abc]
FDvar of LPC	1.00±0.00[a]	-	1.000±0.00[a]	1.000±0.00[a]	0.341±0.29[b]	0.165±0.09[b]	0.171±0.09[b]	0.057±0.01[b]
FDvar of LNC	0.016±0.00[d]	-	0.018±0.00[d]	0.015±0.00[d]	3.01±0.87[ab]	1.51±1.02[c]	2.61±1.10[bc]	4.40±1.10[a]
FDvar of H	0.191±0.019	-	0.222±0.030	0.195±0.001	0.327±0.029	0.415±0.051	0.356±0.042	0.327±0.050
FDvar of LDMC	0.016±0.00[b]	-	0.018±0.00[b]	0.016±0.00[b]	3.203±0.71[a]	3.309±1.29[a]	3.308±1.13[a]	4.254±0.99[a]
FDvar of SLA	0.018±0.002	-	0.020±0.003	0.017±0.002	0.044±0.007	0.466±0.392	0.065±0.009	0.338±0.207
FDvar of WD	0.156±0.017	-	0.181±0.026	0.158±0.013	0.175±0.028	0.460±0.173	0.247±0.032	0.357±0.111

Note: CWM, community weighted average; FDvar, functional divergence; LPC, leaf phosphorus content; LNC, leaf nitrogen content; H, height; LDMC, leaf dry matter content; SLA, specific leaf area; WD, wood density. Different lowercase letters indicate significant differences among different dieback intensity classes of the two areas at $P<0.05$ level. - means no value.

Table 4 Effect of management, dieback intensity and their interaction on taxonomic (richness, evenness and Shannon-Wiener diversity) and structural diversity (mingling, height differentiation and diameter differentiation) indices

Source of variation	df	Species richness		Shannon index		Evenness index	
		F	P	F	P	F	P
Protection (A)	1	193.02	<0.001	32.82	<0.001	744.06	<0.001
Dieback intensity (B)	3	3.12	0.031	6.13	0.001	7.48	<0.001
A×B	3	2.75	0.049	7.49	<0.001	2.97	0.038

Source of variation	df	Mingling index		Height differentiation		Diameter differentiation	
		F	P	F	P	F	P
Protection (A)	1	316.04	<0.001	689.90	<0.001	832.03	<0.001
Dieback intensity (B)	3	9.78	<0.001	18.12	<0.001	28.15	<0.001
A×B	3	2.02	0.118	7.32	<0.001	13.65	<0.001

Protection compared to traditional management caused a significant increase in richness and Shannon diversity indices, and the highest and lowest values were recorded in low and high dieback intensity, respectively. The evenness was higher in the traditional managed area than in the protected area and the highest evenness value was observed in the higher dieback intensity class (Fig. 4). In the traditional managed area, a significant reduction of all structural diversity indices was noted. The highest diameter and height differentiation values were observed in the high intensity dieback and in the protected area, however, there was no clear difference among dieback intensities in the traditional managed area. Moreover, the highest values of the mingling index were observed in the low to high intensity dieback classes of the protected area (Fig. 4).
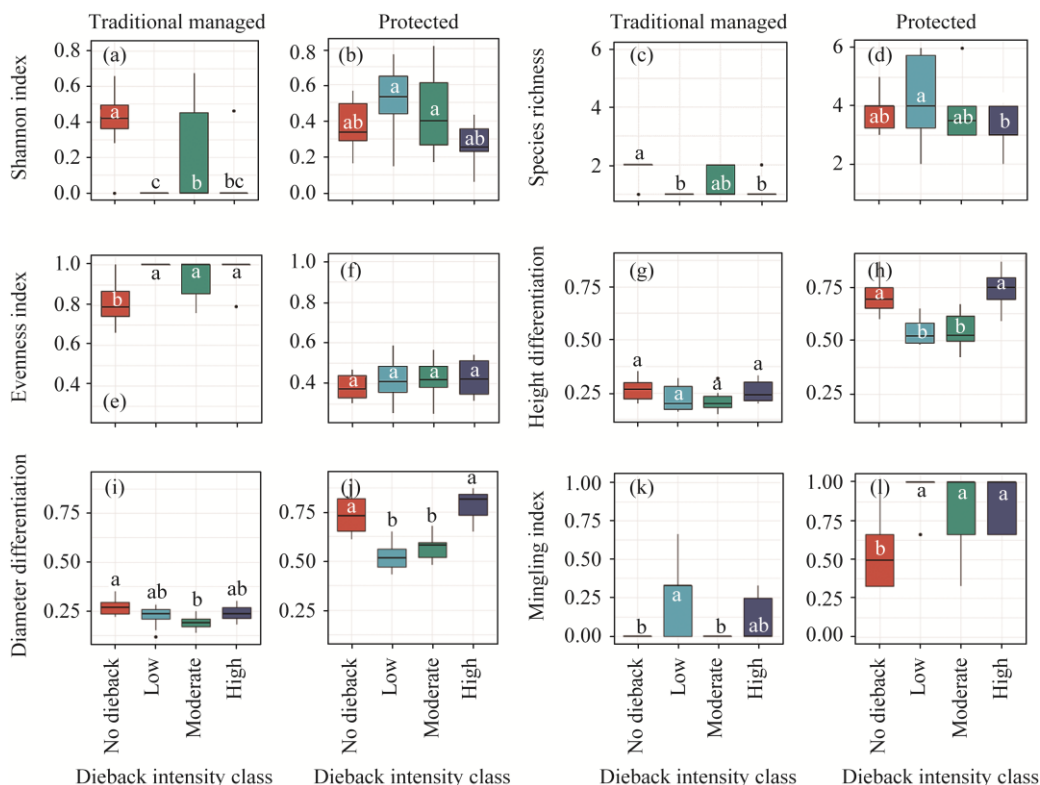
Fig. 4 Mean values of the taxonomic diversity (diversity (a, b), richness (c, d) and evenness (e, f)) and structural diversity (height and diameter differentiation indices (g–j) and mingling (k, l)) indices under different dieback intensity classes (control, low, moderate and high) in the traditional managed and protected areas. Different lowercase letters indicate significant differences among different dieback intensity classes within the same area at *P*<0.05 level.

3.2　Relationships between diversity indices and AGB

We found significant linear relationships for AGB only with the functional diversity indices in the protected area. We noted positive relationships between AGB and CWM of traits such as H, LDMC, SLA and WD and negative relationships with CWM of LPC and FDvar of WD. In the traditional managed area, significant relationships were found only with the taxonomic diversity and structural diversity indices (Fig. 5), either positive (diameter differentiation and species richness) or negative (evenness).

3.3　Structural equation models

The Shannon-Wiener diversity index, mingling index and CWM of LPC had the highest relative importance in each category of plant diversity, stand structure and trait composition (Fig. 6). However, species evenness, mingling index and CWM of LPC provided the best combination predictors in SEM for the protected area. Results showed that AGB was directly and negatively affected by dieback intensity (β= −0.358; *P*=0.006) and trait composition (β= −0.389; *P*=0.002). In addition, dieback intensity positively affected stand structural indices (β=0.363; *P*=0.006). Moreover, structural indices tended to have an effect on trait composition (β=0.287; *P*=0.068; Fig. 7a).

　The evenness, diameter differentiation and CWM of LDMC had the highest relative importance in each category of plant diversity, stand structure and trait composition (Fig. 6), while combination of Shannon-Wiener diversity, diameter differentiation and CWM of LDMC provided the best-fit SEM in the traditional managed area. Dieback intensity had only direct effect on AGB (β= −0.586; *P*<0.001). In addition, dieback intensity had a significant negative influence on taxonomic diversity (β= −0.393; *P*=0.003) and structural indices (β= −0.272; *P*=0.05). In addition, structural indiceshad a strong negative effect on trait composition (β= −0.588; *P*<0.001; Fig. 7b).
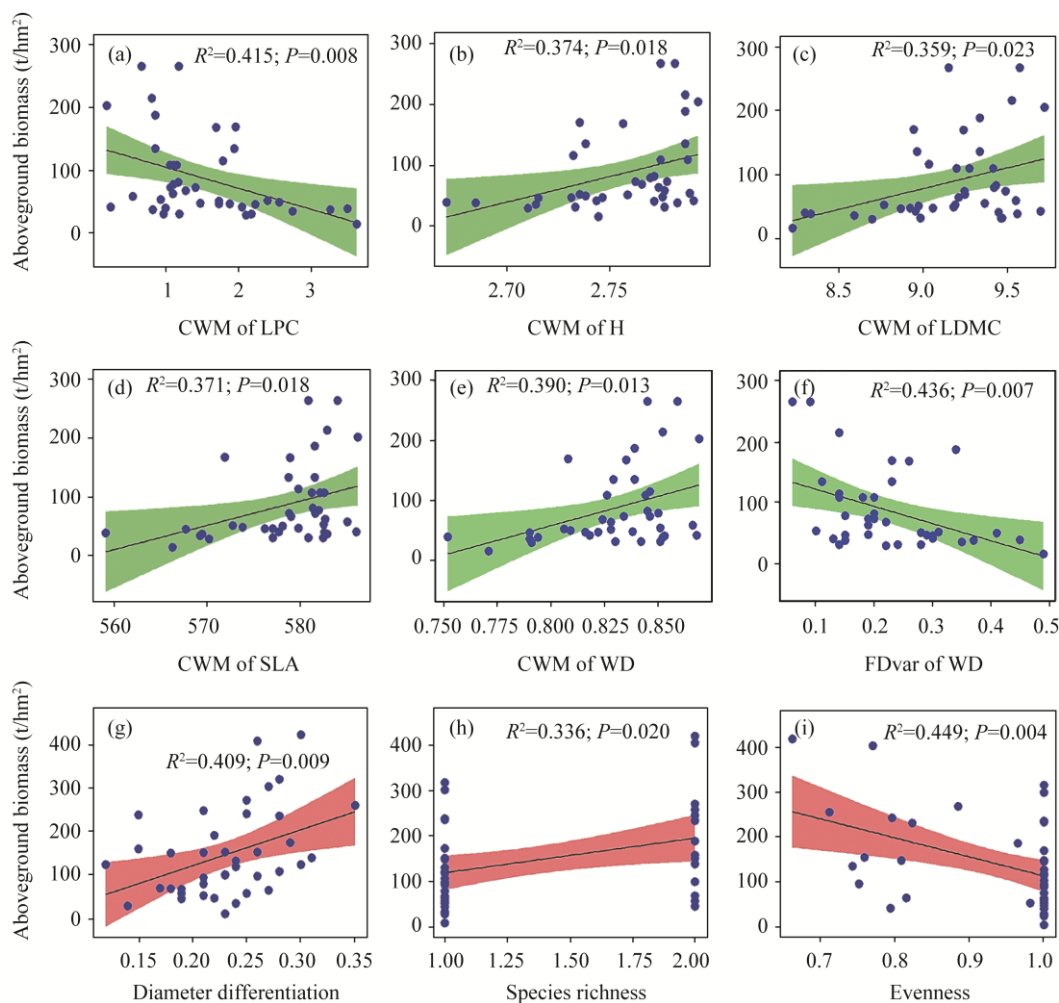
chinaXiv:202203.00035v1

Fig. 5 Relationships between aboveground biomass and functional diversity (CWM (a–e) and Fdvar (f)), taxonomic diversity (structural diversity (diameter differentiation, g), richness (h) and evenness (i)) indices in protected (green confidence interval) and traditional managed areas (red confidence interval)
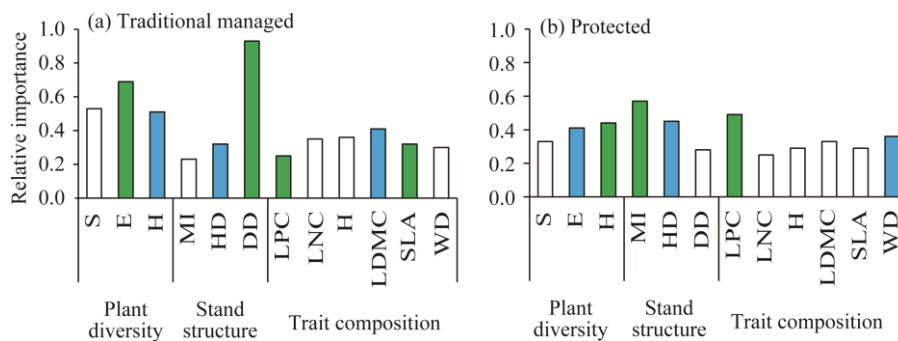

Fig. 6 Relative importance of different variables in each category of plant diversity, stand structure and trait composition of woody species in the traditional managed (a) and protected (b) area; The first and second best parameters for SEM (structural equation modeling) are indicated by green and blue colors. S, richness; E, evenness; H, Shannon-Wiener diversity; MI, mingling index; HD, height differentiation; DD, diameter differentiation; LPC, leaf phosphorus content; LNC, leaf nitrogen content; H, height; LDMC, leaf dry matter content; SLA, specific leaf area; WD, wood density.
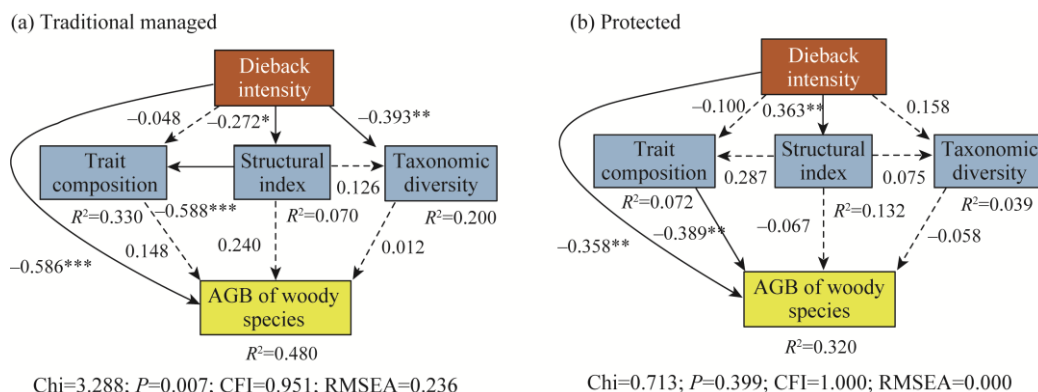
Fig. 7 The best-fit structural equation model linking dieback intensity, taxonomic diversity, stand structural indices and functional trait composition to aboveground biomass of woody species in the traditional managed (a) the protected (b) area. Solid and dashed arrows indicate significant and non-significant paths. For each path, the standardized regression coefficients are indicated by the adjacent values. Chi, chi-square test; R^2, coefficient of determination; CFI, comparative fit index; RMSEA, root mean square error of approximation. *, ** and *** indicate significant differences at $P<0.05$, $P<0.01$ and $P<0.001$ levels, respectively.

4 Discussion

4.1 Effect of management and dieback on diversity and function of ecosystem

We found that the amount of the biomass in the traditional managed area was significantly higher than in the protected area and this difference was especially visible in the no dieback class. This results seems counterintuitive but can be explained by the past management actions. In the traditional managed area, old seed-origin oak trees with a high biomass have been more preserved than those in the protected area (mainly because they provided shade) while other tree species (e.g., *Acer*) as well as shrub species have been exploited for firewood or other uses. Consequently, the access of the remaining trees to ecosystem resources (light, moisture and nutrients) was improved in the absence of competition leading to an increase in growth and biomass. In contrast, growth and biomass accumulation were reduced in the protected area due to the higher interspecific competition but mainly due to the predominance of oaks under the coppice form. Previous studies have shown that trees under the coppice form produced less biomass than seed-origin trees insimilar semi-arid systems (Stojanović et al., 2017; Ozdemir et al., 2019), consistent with these findings.

Evidently, we found that the amount of biomass was reduced along the gradient of dieback intensity in traditional managed area and peaked in the no dieback class where both oak and pistachio trees were present. In contrast, no significant change in biomass was recorded in the protected area among the three classes with symptoms of dieback, indicating that the higher diversity induced by protective measures have moderated the negative impact of dieback on the AGB (Balima et al., 2020; Juřička et al., 2020; Thorn et al., 2020). Besides, tree age (not investigated in this study) is definitely much higher in the traditional managed area, therefore, it is likely that dieback symptoms may worsen in the future in this area.

The CWM values were affected by the type of management and intensity of dieback: CWM of H, LNC and LDMC were higher in the traditional managed area than in the protected area, while CWM of LPC and SLA were higher in the protected area. In the traditional managed area, only old seed-origin oak trees and pistachio trees (more resistant to historical degradation since these large trees are less selectedfor the firewood) were present explaining an increased CWM of H in the community. In the same area, it has been observed that forests exposed to strong human pressure (e.g., harvesting, browsing and grazing) exhibited a simplified vertical structure (reduction of the number of vegetation layers) compared with forests growing under protective measures (Heydari et al., 2017b). As trees were older in the traditional managed area than in the

protected area, they have also produced tougher leaves with a higher lignin content that has increased the LDMC (Chai et al., 2016; König et al., 2018). Previous works have shown that higher LDMC values in a community indicated the predominance of conservative species growing in a low-production environment similar to the traditional managed area in our study (Garnier et al., 2004; Finegan et al., 2015). In the traditional managed area, shrubs such as *C. pontica* and *C. microcarpa* were eliminated to the benefit of oak trees, which developed a more acquisitive resource-use strategy due to the absence of competition and a better access to the ecosystem resources (light, soil moisture and soil nutrients). This can explain the accumulation of elements such as nitrogen in the leaves of these later species, leading to a higher LNC in this area. Similarly, Boukili and Chazdon (2017) reported the prevalence of resource acquisitive traits (such as LNC) in managed forests and conservative traits in old growth forests. Higher values of CWM of LPC and SLA in the protected area can be related to a higher diversity and richness of woody species with the fast nutrient acquisition strategy (Ali and Yan, 2017). In fact, fast-growing species such as wild cherries in this protected area are able to efficiently capture ecosystem resources in a relatively short time.

Contrary to the results of functional composition (CWM), none of the FDvar was affected by dieback intensity, while only FDvar of LNC, LPC and LDMC were influenced by management (protected vs. traditional managed). In this regard, the FDvar values of LNC and LDMC were higher in the protected area than in the traditional managed area, whereas the reverse was true for FDvar of LPC. FDvar generally indicates a difference in the ecological niches of species (Mason et al., 2005). Therefore, the reduced tree diversity due to elimination of the most sensitive species to human disturbances in the traditional managed area has minimized the differences in plant nutrient uptake strategies, while protection has led to the opposite effect, explaining the higher FDvar of LNC and LDMC in the protected area. Similarly, Reich et al. (1995) reported that woody species with different photosynthetic capacities exhibited variations in LNC due to the close relationship between photosynthetic capacities and LNC. We found that management and dieback intensity affected all taxonomic (diversity, richness and evenness) and structural diversity (height and diameter differentiation indices and mingling) indices so that the species richness, Shannon diversity and all indices of structural diversity were higher in the protected area than in the traditional managed area, whereas it was the opposite for evenness.Increased richness and diversity and consequently structural diversity in the protected area is associated with the positive effects of protection on forest ecosystems (Heydari et al., 2017b), which has created the conditions for the emergence and establishment of plant species that are usually less tolerant to disturbances. In contrast, only oak and pistachio trees (in the no dieback class) and only oak trees (in the other dieback classes) remain in the traditional managed area explaining a higher evenness index in these conditions. In line with this result, an increase in species evenness is generally reported after disturbances (Artz et al., 2009; Jin and Han, 2010; Heydari et al., 2020).

Besides, the higher species richness and diversity in the intermediate dieback intensity classes in the protected area confirms the intermediate disturbance hypothesis (Grime, 1973; Connell, 1978), emphasizing the positive role of disturbances of moderate intensity to reduce competition and maximize diversity. In fact, numerous studies examining the effects of various disturbances of moderate intensity, such as fire (Heydari et al., 2017a; Richter et al., 2019), livestock grazing (Levenbach, 2009; Erfanzadeh et al., 2015), land use change (Blaum et al., 2009; Liu et al., 2018), have reported a positive influence on diversity in line with the intermediate disturbance intensity. However, this study is one of the first reportsfor such an effect along a dieback gradient.

Diameter and height differentiation in the protected area were more pronounced than in the traditional managed area particularly in the no dieback and in the high dieback intensity classes. There are contrasting patterns of changes in height and diameter differentiation (both u-shaped) and also species diversity and richness (both hump-shaped) along the dieback gradient in the protected area. The possible more intense competition between woody species in the no dieback site could explain a more pronounced height and diameter differentiation. Heydari et al. (2017b)

and Salehzadeh et al. (2017) also showed that degradation versus protection reduces the diversity and density of woody species, leading to reduced values of the structural indices of diameter and height differentiation, consistent with our results,

4.2 Relationships between diversity indices and AGB

We found significant linear relationships of AGB with CWM and FDvar indices in the protected area, and with taxonomic and structural diversity indices in the traditional managed area. This result emphasizes the importance of using various indices to measure biodiversity, allowing a more comprehensive understanding of links between biodiversity and ecosystem functions (van der Plas, 2019; Zirbel et al., 2019; Garc á-Gir ón et al., 2020). In this area, most of the indices of functional composition (CWM of H, LDMC, SLA and WD) were positively and significantly associated with AGB and these results clearly support the selection effect hypothesis. Similar findings have largely been reported, for instance, Finegan et al. (2015) reported a positive relationship between CWM of H and AGB in tropical forests (Garnier et al., 2004; Finegan et al., 2015; Ali and Yan, 2017; Tahmesebi et al., 2017). In contrast, we found a negative relationship between FDvar of WD and AGB in the protected area, which is in contrast with the study of Ali and Yan (2017) who reported a positive relationship between functional divergence of twig WD (FDvar of twig WD) and AGB in a secondary forest. Overall, this relationship between FDvar of WD and AGB as well as the relationship between functional composition (CWM) and AGB, emphasize the large impact of the dominant tree species on biomass production in this semi-arid forest ecosystem. In fact, in the protected area, stands where the dominant species prevails (typically oak trees with a high WD) present a higher biomass than stands with a mixture of oaks and other tree species with a low WD. As previously stated, this result reinforces the selection effect hypothesis.

In the traditional managed area, AGB was positively associated with species richness and diameter differentiation but negatively with evenness. In this area, only oak and pistachio trees are found among different dieback intensity classes. When the two species are present, both the diameter differentiation and the above ground biomass increase. In contrast, in the protected area, species composition is more stable across the different dieback intensity classes and only the relative abundance changes. Consequently, diameter differentiation remains low and not significantly related to AGB. The negative relationship between AGB and evenness found in this study is in line with numerous previous works reporting a similar trend between various ecosystem functions and evenness (Kardol et al., 2010; Vance-Chalcraft et al., 2010; van Con et al., 2013), confirming the selection effect hypothesis again. In fact, an increase in evenness indicates a reduced abundance of the dominant species leading to a reduced role of these species in ecosystem functions. In our study, the analysis of the relationships between different biodiversity indices and AGB provides clear evidence to support the selection effect hypothesis and emphasizes the importance of the dominant species in ecosystem function. In contrast, we found no evidence of a positive effect of niche complementarity on biomass.

5 Conclusions

The relationships between different aspects of diversity (taxonomic, structural and functional) and AGB (a major component of global carbon balance) have been studied extensively but rarely under the simultaneous influence of forest dieback intensity (i.e., low, moderate and high) and management conditions. Our results emphasize that the use of different approaches for diversity quantification is vital to assess changes in AGB of forest systems subjected to various intensities of management and disturbances. Along a dieback intensity gradient, the leaf functional traits are efficient predictors in estimating AGB in the protected forests, while taxonomic and structural indices provide better results in the forests under a high human pressure. The results clearly reveal that natural disturbances (here dieback intensity) play a major role in driving ecosystem productivity as well as biotic conditions. Lastly, our results clearly support the selection effect

hypothesis as most of the biomass accumulation is the result of the dominant species, i.e., Brant's oak.

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